

RECOVERY RATES OF CRYPTOBIOTIC CRUSTS: INOCULANT USE AND ASSESSMENT METHODS

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ABSTRACT—Recovery rates of cyanobacterial-lichen soil crusts from disturbance were examined. Plots were either undisturbed or scalped, and scalped plots were either inoculated with surrounding biological crust material or left to recover naturally. Natural recovery rates were found to be very slow. Inoculation significantly hastened recovery for the cyanobacterial/green algal component, lichen cover, lichen species richness, and moss cover. Even with inoculation, however, lichen and moss recovery was minimal. Traditional techniques of assessing recovery visually were found to underestimate time for total recovery. Other techniques, such as extraction of chlorophyll *a* from surface soil and measurement of sheath material accumulation, were used and are discussed.

Key words: cyanobacteria, soil algae, cryptobiotic crusts, cryptogamic crusts, recovery, disturbance, reclamation, inoculation, *Microcoleus vaginatus*.

Cyanobacterial soil crusts occur in semiarid and arid regions throughout the world. Studies of these crusts have documented the importance of the role they play in these ecosystems. This role includes the stabilization of soils (Belnap 1990, Harper and Marble 1985, Marathe 1972), improved nutrient status of vascular plants growing in the crust (Belnap and Harper unpublished), and improved soil structure (Metting and Rayburn 1983).

For the National Park Service, maintaining the biota and visual aesthetics of undisturbed landscapes is a central concern. Since cryptobiotic crusts are widespread throughout parks on the Colorado Plateau and damage to them is highly visible, finding methods to hasten the recovery of disturbed crusts is of importance to this agency. The use of inoculants to speed up recovery of these crusts has been reported by several authors (Ashley and Rushforth 1984, Lewin 1977, St. Clair et al. 1986, Tiedemann et al. 1980).

Traditionally, assessment of recovery rates of cryptobiotic soil crusts after disturbance has been based on visual measurements only. Generally, such measurements have included percent cover of the cyanobacterial/green algal, lichen, and moss components; presence of pedicled soil surfaces; and number of moss and lichen species observed (Anderson, Harper, and

Holmgren 1982, Anderson, Harper, and Rushforth 1982, Brotherson et al. 1983, Cole 1990). Unfortunately, visual measurements cannot quantify the amount of the cyanobacteria/green algae present, since filaments and cells ramify through several millimeters of surface soils. The few studies that have attempted to quantify the amount of cyanobacteria and green algae tissue present have used fluorescence optics or culturing (Ashley and Rushforth 1984, Johansen and Rushforth 1985). Both methods have problems associated with them: fluorescence optics is very time consuming, and culturing may give misleading results. Recently, Beymer and Klopatek (1992) used chlorophyll *a* to estimate cyanobacterial and green algal tissue in recovering crusts.

Another aspect of crust recovery should also be considered. *Microcoleus vaginatus*, the cyanobacterium that makes up the bulk of crustal organisms in the semiarid environments considered here, may contribute up to 95% of the crust biomass (Belnap personal observation). This cyanobacterium secretes a thick, extracellular gelatinous sheath around the living filaments. This sticky sheath material adheres to soil particles, thereby aggregating them into larger, less erodible particles (Belnap and Gardner 1993, Harper and Marble 1985). When moistened, the filaments of *Microcoleus* are partially extruded from the colonial sheaths; the filaments

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produce may sheath around themselves and leave the abandoned sheath material behind. Consequently there is much more abandoned than currently inhabited sheath material in a well developed crust (Belnap and Gardner 1993). Since abandoned sheath material still adheres to and binds together soil particles, it continues to contribute to soil stability and may increase moisture and nutrient retention in these soils (Belnap and Gardner 1993). Thus, any assessment of recovery of crusts should consider the amount and condition of both abandoned and occupied sheath material present.

The purpose of this study was twofold. The first was to establish whether inoculation using nearby biotic crustal material could be used to increase biotic recovery rates of disturbed crusts. The second was to examine other methods of assessing crust recovery. These included (1) using chlorophyll *a* to quantify living cyanobacterial/algal components of the crusts, (2) measuring height of biologically induced microrelief, and (3) assessing accumulated sheath material.

METHODS

Studies were conducted on sandy and gypsiferous substrates. Plots were established in four places: (1) on a gypsiferous substrate in Arches National Park (ARCH), about 20 miles northwest of Moab, Utah, in 1985; (2) on a sandy substrate at Sand Flats (SF), 5 miles east of Moab in 1987; (3) on a sandy substrate in the Behind-the-Rocks (BTR) area, 10 miles south of Moab in 1985; and (4) on a sandy substrate at the Island-in-the-Sky (ISKY) district, Canyonlands National Park, about 20 miles northwest of Moab in 1985. At the ARCH and ISKY sites, 0.25 m² plots were randomly assigned to one of two treatments (disturbed or undisturbed, and replicated 7 (ARCH) and 5 (ISKY) times). The undisturbed treatment consisted of scalping the top 3 cm of soil. If all of the disturbed sites were first randomly selected for inoculation, inoculation consisted of crumbling the scalped material and adding 500 cc of the mixture (one cubic decimeter) to each plot. Chlorophyll *a* levels in the inoculum were determined. At the BTR and SF sites chlorobacterial algal inoculum was added to the plots. At the BTR site plots were replicated 5 and 7 times. No plots were inoculated at the SF, ARCH, and ISKY sites. Scalped plots were replicated 7 times at each site. Plots

were 0.25 m² in area, three were 0.5 m², and two were 0.75 m².

Sites were sampled in 1990. Since plots were established at various times during the 1985–88 period, different recovery periods were represented. Gypsiferous plots at ARCH and sandstone plots at ISKY were sampled after two years, SF plots were sampled after three years, and BTR sites were sampled after five years. Measurements consisted of 5–10 samples of crust (cores 1 cm deep by 1.6 cm in diameter) collected from each plot. Chlorophyll *a* in these samples was extracted with dimethyl sulfoxide (DMSO); this extract was centrifuged and spectrophotometrically analyzed at an optical density of 665 nm.

Visual estimates of cryptobiotic cover were taken at all sites as well. Percent cover of cyanobacteria/green algae, mosses, and lichens was recorded for all treatments at all sites. Height of pedicellation (measured from the highest point of the pedicel to the ground surface between pedicels) and thickness of the crust (depth to which the sheaths of *Microcoleus* could be detected) were measured at the BTR site. Thickness of the crust was measured by slicing through the crust with a razor blade. In the coarse, sandy soil found at the BTR site, sand not bound by gelatinous sheath material fell away freely, enabling one to estimate the depth to which sheath material was present.

Data were analyzed for significance using an unpaired Student's *t* test to compare inoculated with uninoculated plots; ANOVA and Duncan's multiple range test were used to distinguish significant differences between uninoculated, inoculated, and control plot values. Each characteristic was run separately (chlorophyll *a*, lichen and moss cover, and richness). Probabilities of <.05 were considered statistically significant.

RESULTS

All parameters measured for all treatments at all sites were statistically different ($p < .001$) except for the visual assessment of cyanobacterial/green algal cover. For this characteristic all surfaces at all sites appeared to be 100% covered within a year. In uninoculated plots the cyanobacterium *Microcoleus vaginatus* was always the first to develop observable cover. In all disturbed plots where any lichens were observed, the lichen *Collema tenuax* was always present.

TABLE 1. ARCH site: average values for selected parameters of cryptobiotic crusts following various treatments. Recovery interval was 2 years. See text for details of treatments and biotic variables. All differences are statistically different at the $p < .05$ level, except moss cover (all values zero).

Treatment	Absorption by chlorophyll <i>a</i>		Lichen cover		Lichen species		Moss cover	
	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.
Control	0.14	0.03	43.3	12.1	4.3	0.3	0.0	0.0
Inoculated	0.05	0.02	3.6	2.9	2.6	0.5	0.0	0.0
Uninoculated	0.03	0.001	1.3	1.5	1.8	0.4	0.0	0.0

TABLE 2. BTR site: average values for selected parameters of cryptobiotic crusts following various treatments. Recovery interval was 5 years. See text for details of treatments and biotic variables. All differences are statistically different at the $p < .05$ level.

Treatment	Absorption by chlorophyll <i>a</i>		Lichen cover		Lichen species		Moss cover	
	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.
Control	0.09	0.07	23.2	3.0	4.4	0.9	11.6	3.2
Uninoculated	0.01	0.01	0.0	0.0	0.0	0.0	0.0	0.0

Arches

Plots at this site were scalped and either inoculated with nearby biotic crustal material or not inoculated. Chlorophyll *a* and visual characteristics were measured after two years. All biotic aspects of recovery on this gypsumiferous substrate were significantly enhanced by inoculation, including chlorophyll *a* concentrations, percent cover of lichens, and number of lichen species present (Table 1). Chlorophyll *a* in undisturbed crusts was almost twice that of inoculated plots (0.14 vs. 0.077), and almost five times that of uninoculated crust (0.14 vs. 0.03). Lichen cover averaged 43.3% on undisturbed plots, 3.6% on inoculated surfaces, and 1.3% on uninoculated surfaces (all differences are statistically significant). Lichen species on undisturbed areas averaged 4.3 per plot, while on the inoculated surfaces this average was 2.6. Uninoculated surfaces averaged 1.8 species per plot. No mosses were present on any surfaces. The only exception to these significant differences between treatments was the visual assessment of the cyanobacterial/green algal cover. All treatments gave the appearance of 100% coverage within one year.

Behind-the-Rocks

Plots at this site were either scalped or left undisturbed. No plots were inoculated. Measurements were taken five years later. After this time period all parameters measured showed large and statistically significant differences between the undisturbed and uninoculated, scalped areas (Table 2). Visually, the scalped areas looked well on their way to recovery. The entire surface area of scalped plots appeared covered by cyanobacteria, and pedicellation had begun. Pedicel height in undisturbed crusts ranged from 4.3 to 7.9 cm, averaging 4.9 cm. In scalped plots, pedicels averaged 2 cm in height, or about 41% of the average pedicel height on undisturbed plots. From this, one might assume that the cyanobacterial/green algal component was 41% recovered. However, chlorophyll *a* levels and the thickness of sheath accumulation necessitate a different interpretation. Chlorophyll *a* levels were still only 12% of those in undisturbed sites after five years. Measurements of depths to which accumulated sheath material could be detected demonstrated that on scalped plots, though pedicels averaged 2 cm in height, thickness of sheath material was only 0.6–0.9 cm, averaging 0.8 cm. Over half the volume of the average pedicel consisted of loose

TABLE 3. (F-K) (5) Recovery of crust following scalped parameters of cryptobiotic crusts following various treatments. Recovery measured over 2 years. S = 0.000000001 (6) treatments and biotic variables. All differences are statistically different at the $p < 0.05$ level.

Treatment	Absorption by chlorophyll <i>a</i>		Lichen cover		Lichen species		Moss cover	
	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.
Control	0.11	0.02	7.3	3.1	0.9	0.3	7.3	3.4
Inoculated	0.02	0.01	1.5	1.5	0.7	0.5	1.2	1.5
Uninoculated	0.002	0.001	0.3	0.5	0.3	0.5	0.0	0.0

TABLE 4. SE (SD) average values for selected parameters of cryptobiotic crusts following various treatments. Recovery measured over 3 years. See text for details of treatments and biotic variables. All differences are statistically different at the $p < 0.05$ level.

Treatment	Absorption by chlorophyll <i>a</i>		Lichen cover		Lichen species		Moss cover	
	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.
Control	0.3	0.05	42.5	12.9	4.3	1.1	12.1	10.5
Uninoculated	0.02	0.001	1.5	1.1	1.1	0.6	0.09	0.3

sand. On the other hand, in undisturbed plots sheath material occurred throughout the volume of the pedicels, and little loose sand was found. In the undisturbed crust sheath material was observable at an average depth of 4.9 cm, or six times the depth measured in the scalped areas. The difference was highly significant statistically.

Lichen cover showed no recovery at all; while undisturbed sites averaged 23.2% cover, no lichens were found in the scalped plots after five years. An average of 4.4 lichen species were found on the undisturbed plots, while none were found in the scalped plots. Moss cover likewise showed no recovery, though undisturbed plots averaged 11.6% moss cover (Table 2).

Island-in-the-Sky

Control sites were scalped and then either reestablished with surrounding crust material or left undisturbed. Chlorophyll *a* measurements were made three years after treatment. Levels of chlorophyll were significantly different ($p < 0.000000001$) between uninoculated, and inoculated areas. Uninoculated plots averaged chlorophyll levels of less than 2% of those observed in undisturbed plots, while inoculated plots averaged about 22% of the amount of undisturbed plots. Lichen cover was calculated

areas averaged 7.3%. Inoculated plots had significantly less lichen cover (1.8%), and uninoculated plots averaged 0.3% lichen cover. The same pattern was observed for moss cover: undisturbed plots averaged 7.3%, inoculated plots averaged 1.2%, while uninoculated plots had no moss cover at all. Visual assessment of the cyanobacterial/green algal cover was rated as 100% after one year for all treatments.

Sand Flats

Plots at this site were either scalped or left undisturbed, with measurements taken three years later. As with the other sites, all parameters were significantly different between scalped and undisturbed plots (Table 4). Chlorophyll *a* levels in the scalped areas were only 8% of those observed in the undisturbed areas (0.022 vs. 0.275) after three years. Reestablishment of lichens was again exceptionally slow: after three years, scalped plots had only 1.5% lichen cover compared to 42.5% cover found in nearby undisturbed areas. Scalped plots averaged only 1.0 lichen species per plot, while undisturbed areas averaged 4.3. Moss cover was slow to recover as well. While undisturbed areas had an average of 12.1% cover, the disturbed areas averaged 0.09% cover. As with the other areas, visual

assessment of cyanobacterial/green algal cover reached 100% within one year.

DISCUSSION AND CONCLUSION

It is clear from these results that inoculation can hasten the biological recovery of disturbed crusts. Inoculated plots had far greater chlorophyll *a* concentrations than uninoculated plots, indicating a larger establishment of cyanobacteria and green algae. They also had significantly greater lichen species richness and greater lichen and moss cover than uninoculated plots. It should be noted, however, that although lichen cover and moss cover were significantly greater on inoculated than uninoculated plots, recovery for both lichens and mosses was extremely slow for both treatments.

Inoculation hastened some aspects of visual recovery of the cyanobacterial/green algal component. Areas that had been inoculated had greater pedicellation sooner than areas that were not inoculated. Apparent coverage of the soil surface by this crustal component, however, was not hastened by inoculation, since all soil surfaces appeared completely covered within one year. Inoculation somewhat hastened the visual recovery of the lichens and mosses; however, absolute differences were so small that it was difficult to tell treatments apart without close examination.

The use of spectrophotometrically determined chlorophyll *a* in surface soil as a measure of recovery of cryptobiotic crusts proved to be a time-efficient and reliable measure. When comparing different treatments or areas, however, one must take all samples within a short period of time to eliminate seasonal variations in chlorophyll *a* as a potentially confounding variable.

Visual assessment as a means of determining crust recovery proved to be misleading. All plot surfaces, whether inoculated or not, appeared completely covered by cyanobacteria, and most showed rudimentary pediceling after only one year. This gave the impression that the cyanobacterial/green algal components of the crusts were mostly or fully recovered. Chlorophyll *a* measurements, however, told a different story: dramatic differences in chlorophyll *a* levels demonstrated that the amount of photosynthetic cryptobiotic tissue present differed greatly among treatments. Uninoculated plots sometimes supported only 2% as much chlorophyll *a* as was found in nearby undisturbed

crusts. Visual assessment also did not accurately assess the accumulation of abandoned sheath material. The method employed in this study to measure the gelatinous sheath material accumulated was not completely satisfactory in that it worked well only in dry, coarse-grained soils. Some other means of assessing this crustal characteristic must be developed to be used on all types of substrates. This assessment should take into account both the amount of polysaccharide material present as well as its structural integrity. The bulk of microbiotic tissue in sandy soils consists of abandoned, buried sheath material. Though abandoned, this sheath material probably reduces soil erodibility and enhances moisture and nutrient retention of the soil. Any damage to such abandoned material, however, is non-repairable, since living filaments are no longer present to re-secrete the gelatinous material. Repeated trampling of this brittle material pulverizes the abandoned sheaths, breaks up their connections to sand grains, and probably hastens aggregate dissolution. For this reason, assessment of recovery from disturbance should consider not only the presence of living organisms and the amount of abandoned sheath material present, but also the integrity, or condition, of the sheath material. In places where all or most sheath material has been removed (such as construction sites), assessment of crustal integrity and depth is much simplified. However, in situations where sheath material is repeatedly trampled in place, quantification of the crustal condition is much more difficult. Chemical analysis of sheath material will not give us information about the integrity of that material; yet quantification of integrity is critical to any assessment of crustal recovery and resultant stability of the system.

Prior estimates of time for natural recovery of cryptobiotic crusts from disturbance have varied widely, ranging from a few years to 100 years for full recovery of all components (Anderson, Harper, and Rushforth 1952, Callison et al. 1955, Cole 1990, Jeffries and Klopatek 1957, Johansen et al. 1952, 1954). In this study it is clear that if only visual estimates of cyanobacterial cover are considered, recovery appears quite rapid, whether sites are inoculated or not. This is generally supported by other studies that utilized visual assessments (Cole 1990, Johansen and Rushforth 1955), where recovery was reported in up to five years. However, there has been an exception—Johansen et al. (1954), who

recovery of cyanobacteria succeeding before visual aspects.

Other aspects of crustal recovery, such as chlorophyll *a* levels, microbiotic enumeration, depth ramified by thickness of accumulated sheath materials, or lichen and moss species and cover, generally occur much more slowly (Anderson, Harper, and Rushforth 1982, Callison et al. 1985, Harper and Marble 1985, Jeffries and Klopatek 1987, Johansen and St. Clair 1986). Chlorophyll *a* levels increased 1% a year at the ESKY site, while at other sites they increased approximately 2.4, 2.5, and 2.6% a year. Assuming a linear accumulation rate and the greatest rate of increase observed, full recovery of chlorophyll *a* levels would take about 40 years. At the BTR site depth ramified by sheath material ranged from 1.2 to 1.5 mm a year. If one assumes this accumulation process to be linear, and that temperatures and moisture conditions during the interval considered were fairly typical, recovery from disturbances that destroy accumulated sheath material may take longer. Attaining the average depth of ramification of surface soil observed here would take 30–40 years for full recovery. Maximum depths observed would require 40–65 years at the rates observed. Natural recovery rates of lichen and moss were much slower than those for cyanobacterial cover, chlorophyll *a* levels, or sheath depths. Lichens showed some recovery at three of the four sites. At observed rates full recovery at these three sites would take 45–55 years. At the BTR site no recovery was seen, even after five years, and so time to full recovery is impossible to predict. Moss recovery was much slower than that of the lichens. At two of the three sites where mosses were found, no moss recovery at all was seen. This makes prediction of recovery rates impossible, but clearly these rates are extremely slow. At the third site, where some recovery was seen, full recovery of moss cover would take over 250 years at the average rate of recovery. Recovery rates of all members of crustal communities depend on several factors. The type and extent of disturbance will greatly influence time to recovery. Areas that are compacted, lightly or infrequently used, or are surrounded by a fence, thereby excluding animals, would experience such as patchy, irregular, or low-intensity sources close by to limit recovery (Callison 1980, Johansen et al. 1982, 1986). Thus, identification of environmental variables will improve recovery. Since these organisms are also microbially

active when wet, years with higher effective precipitation will show faster recovery than years with lower effective precipitation (Behnke personal observation, Johansen et al. 1984, 1993). Different substrates (gypsiferous and sandy soils) did not affect recovery rates of cyanobacteria, mosses, or lichens in this study.

Much work remains to be done in the assessment of crustal recovery. Since recovery rates depend on type and extent of disturbance, availability of nearby inoculation material, and temperature and moisture regimes that follow disturbance events, the relative effect of all these factors must be better understood before managers can accurately estimate recovery rates at specific sites. In addition, more work is needed on ways to assess recovery, including linkage of chlorophyll *a* measurements and algal enumeration techniques, and inclusion of sheath integrity measurements. Also, more research should be directed at recovery rates for crusts on different substrates and with different floral compositions. This study demonstrates that recovery can take a long time, especially for lichen and moss components of cryptobiotic crusts. For this reason, a conservative approach should be adopted relative to activities that may disturb these crusts. More effort should be devoted to evaluating procedures that will hasten reestablishment of cryptobiotic crusts, such as inoculation with pulverized natural surfaces or artificially grown inocula.

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